

## Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

### Original Article

# Environmental and parental control of Pacific sardine (*Sardinops sagax*) recruitment<sup>†</sup>

Juan P. Zwolinski<sup>1\*</sup> and David A. Demer<sup>2</sup>

<sup>1</sup>Institute of Marine Sciences, University of California, Santa Cruz, Earth and Marine Sciences Building, Rm A317, Santa Cruz, CA 95064 (affiliated to SWFSC), USA

<sup>2</sup>Fisheries Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA

\*Corresponding author: tel: +1-858-546-5654; fax: +1-858-546-5652; e-mail: [juan.zwolinski@noaa.gov](mailto:juan.zwolinski@noaa.gov)

Zwolinski, J. P., and Demer D. A. Environmental and parental control of Pacific sardine (*Sardinops sagax*) recruitment. – ICES Journal of Marine Science, 71: 2198–2207.

Received 4 April 2013; accepted 17 September 2013; advance access publication 18 October 2013.

We confirm that sardine recruitment in the California Current, during the last three decades, mimics aspects of the environment in the North Pacific indicated by the Pacific Decadal Oscillation (PDO) index. The periods of stock increase and decrease followed consecutive years with positive and negative PDO values, respectively. During the “warm” periods, the average number of recruits per biomass was more than threefold higher than that during the “cold” periods. In addition to the environmental conditions experienced by the sardine larvae, we show that the variability in sardine recruitment is partially explained by the environmental conditions many months before the spawning season and the adult condition factor. We hypothesize that sardine have a metabolic deficit during spawning, so prior good feeding opportunities are necessary to increase both total fecundity and offspring robustness, to enhance both reproduction and survival, respectively. Our findings augment a century-old theory that the reproductive success of small pelagic fish is governed by the survival of the early life stages. The condition of each parent also matters. To predict sardine recruitment, we propose a “dual-phase” model based on seasonal PDO-based indices and a condition factor. The model identifies summer feeding seasons conducive to a good adult condition factor followed by spring-spawning seasons supportive of good larval retention and growth.

**Keywords:** condition factor, environment, fecundity, prediction, spawning.

### Introduction

The northern stock of Pacific sardine (*Sardinops sagax*) off the west coast of North America has exhibited multiple dramatic boom and bust cycles [see Zwolinski and Demer (2012) for two recent examples]. Although the underlying mechanisms for these cycles remain uncertain, it is broadly acknowledged that the environment plays a principal role (Jacobson and MacCall, 1995; MacCall, 2009; Zwolinski and Demer, 2012). For example, from the 1950s to the 1970s, when sardine productivity and abundance were low, the

seawater temperature in the northeastern Pacific was lower than in the previous and subsequent decades (MacCall, 1979; Barnes *et al.*, 1992). This observation led Jacobson and MacCall (1995) to model the reproductive success of sardine vs. sea surface temperature (SST) in the main sardine spawning area. For practical reasons, the modelled temperature was then indexed to the long-term time-series of SST measured at Scripps Institution of Oceanography (SIO) pier and provided a foundation for the first environmentally driven decision rule for the exploitable fraction of a fish population

<sup>†</sup>This article does not necessarily reflect the official views or policies of the National Marine Fisheries Service, the National Oceanic and Atmospheric Administration, the Department of Commerce, or the Administration.

(PFMC, 1998). The aim was to reduce fishing pressure during years of low productivity and increase it during years of surplus production. However, from 2006 to 2012, despite the high SST values measured at the SIO pier, there were successive recruitment failures, fishing continued, and the stock biomass dropped to the lowest level in the most recent two decades (Zwolinski and Demer, 2012).

McClatchie *et al.* (2010) re-evaluated Jacobson and MacCall's (1995) SST-to-recruitment relationship and concluded that SST measured at the SIO pier and recruitment success (number of recruits per unit of parental biomass) were no longer correlated. They also noted a disconnection between the temperature measured at the SIO pier and that of the major sardine spawning grounds. These differences may explain why other studies have provided evidence of strong correlation between the assessed sardine recruitment and the seawater temperatures offshore (e.g. Galindo-Cortes *et al.*, 2010; Lindegren and Checkley, 2013). More generally, many other studies have shown that fluctuations in atmospheric and oceanographic conditions matched, in both period and phase, oscillations in small pelagic fish biomasses in the California Current and elsewhere (Jacobson *et al.*, 2001; Peterson and Schwing, 2003; King, 2005; MacCall *et al.*, 2005; Norton and Mason, 2005; Wells *et al.*, 2006; Deyoung *et al.*, 2008; Alheit and Bakun, 2010; Overland *et al.*, 2010; Perry *et al.*, 2010; Irvine and Fukuwaka, 2011). Therefore, it appears that environmental dynamics do affect the productivity and community structure of marine organisms, particularly small coastal pelagic fish species (CPS; Fréon *et al.*, 2005; Alheit and Bakun, 2010; Zwolinski and Demer, 2012), and the challenge is to identify the mechanisms.

Mantua *et al.* (1997) introduced the Pacific Decadal Oscillation (PDO), an index that tracks a pattern in the SST of the north Pacific that fluctuates at multidecadal scales and which describes environmental dynamics that have profound effects on the recruitment and biomass of certain salmon stocks in Alaska. The environmental dynamics reflected by the PDO were also related to the total biomass and diversity of copepods off northern California (CA) and Oregon (OR), which in turn have strong impacts on the local salmon recruitment (Peterson and Schwing, 2003). Concurrently, Chavez *et al.* (2003) analysed low-frequency oscillations in CPS abundances in the 20th century and concluded that cold periods off the west coast of the United States, implicitly described by the PDO, were coincident with decades of anchovy dominance. Conversely, warm periods, also indicated by a positive PDO, were associated with decades of sardine dominance. Chavez *et al.* (2003) noted that the principal characteristics of the multidecadal "sardine regimes" in the northeastern Pacific were: warmer than average SST, strong stratification, low nutrients in the photic layer, and low overall productivity, and more frequent *El Niño* Southern Oscillation (ENSO) episodes. They also suggested pathways through which the environment could affect the epipelagic community.

Rykaczewski and Checkley (2008) advanced a mechanistic approach to hindcast surplus sardine production. They showed that sardine surplus production, which is directly related to reproductive success, is significantly correlated with the intensity of curl-driven upwelling offshore of southern CA during spring and summer (May–July). Their work supports a century old theory that the survival of early life stages, mediated by their environment, controls recruitment success for sardine and other CPS (Hjort, 1914; Cury and Roy, 1989; Cury *et al.*, 2000). However, Zwolinski and Demer (2012) found that the condition factor of adult sardine, which is an indicator of their forthcoming total fecundity (Marshall *et al.*, 1999), may also help to predict recruitment. Their observation emphasized the importance of parental condition to successful reproduction via

both increased fecundity and more robust and resilient offspring (Riveiro *et al.*, 2004; Garrido *et al.*, 2008). Mechanistically, sardine tend to rely principally on fats and proteins stored prior the spawning season to provide energy for the protracted energy expenditure (Ganias *et al.*, 2007).

Lindegren and Checkley (2013) updated the analyses done by Jacobson and MacCall (1995) and McClatchie *et al.* (2010) and found that the spring and annual averages of the SST measured offshore during the California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys during the spawning year are explanatory variables for sardine recruitment and the recruitment-to-parental biomass ratio. However, in their analysis the larger scale multivariate ENSO and PDO indices did not perform as well as the regional offshore temperature.

To explain why the local environmental indices out-performed the large-scale indices, we hypothesize here that the reproductive success of sardine is determined by a sequence of environmental conditions initiated many months before the spawning season, continuing through the larval period. If correct, then environmental indicators for feeding conditions during summer, and those for larval retention and growth the following spring, should collectively predict recruitment. In this paper, we propose such a "dual-phase" environmental indicator, based on the averages of the monthly PDO index, which may predict sardine recruitment.

## Methods

To investigate the environmental drivers of sardine recruitment, we first explored the correlation between the logarithmic reproductive success (the logarithm of the number of recruits per unit of spawning biomass; Jacobson and MacCall, 1995) and each of three large-scale indices and one regional oceanographic index. We then fit a formal stock–recruitment model, allowing for environmental dependence (Jacobson and MacCall, 1995). Using the best model, we reconstructed the time-series of sardine recruitment in the 20th and 21st centuries, for years with available estimates of biomass. Finally, we included the adult condition factor in the environmental stock–recruitment model and evaluated its relative performance. The adult condition factor may control the reproductive output and thereby the recruitment success (Zwolinski and Demer, 2012). The data and modelling procedures are explained in detail below.

## Recruitment and biomass data

Using the results of the 2010 stock assessment model (Hill *et al.*, 2010), recruitment ( $R$ ) was estimated by the abundance of age-0 sardine in July, and the parental stock of sardine ( $S$ ) was estimated by the biomass of age-1 and older (age-1+) sardine in January of the same year, from 1981 to 2011. We used the 2010 assessment model because its results, or results from earlier models with the same configuration, have been used previously to evaluate the dependence of sardine recruitment on the environment (Galindo-Cortes *et al.*, 2010; McClatchie *et al.*, 2010; Lindegren and Checkley, 2013).

## Condition factor data

Currently, the majority of the sardine spawning population migrates seasonally to feed during summer and autumn in the productive areas off OR, WA, and VI (Zwolinski *et al.*, 2011; Demer *et al.*, 2012). These migrations appear to allow sardine to store fat for use during the subsequent reproductive season. The condition factor [ $k$ ;  $k = 10^5 \times \text{body weight (g)}/\text{standard length}^3 \text{ (cm)}$ ], related to the amount of body fat, may be a proxy for reproductive output and thus sardine recruitment (Zwolinski and Demer, 2012). For the period 1999–2007, values of  $k$  for the migrating portion of the stock were estimated from the OR and Washington (WA) fishery

statistics. The average  $k$  values for each year were estimated from predominantly adult sardine (standard length, SL,  $\geq 160$  mm) landed there between August and October before each recruitment year.

### Environmental data

We used three remotely-sensed large-scale environmental indices evaluated monthly: the multivariate *El Niño* index (MEI; <http://www.esrl.noaa.gov/psd/enso/mei/table.html>; Wolter and Timlin, 1998); the PDO (<http://jisao.washington.edu/pdo/PDO.latest>; Mantua *et al.*, 1997); and the North Pacific Gyre Oscillation (NPGO; <http://www.o3d.org/npgo/npgo.php>; Di Lorenzo *et al.*, 2008). These three variables were selected based on previous recognition of their ability to summarize multiple oceanographic variables in the northeast Pacific that are relevant to the dynamics of CPS (Mantua *et al.*, 1997; Peterson and Schwing, 2003; Di Lorenzo *et al.*, 2008; King *et al.*, 2011). To represent the environmental conditions encountered by adult sardine during their summer feeding season, we averaged these indices during summer (August through October) before the spawning season. To represent the environmental conditions experienced by the early life-stages, we averaged the indices during spring (March through July) of the spawning (and recruitment) year. To represent the environmental conditions experience by the adult and early life-stage sardine, we summed the two seasonal PDO indices.

Although we aimed to investigate any relationships between these indices of large-scale oceanographic phenomenon and sardine recruitment, we also analysed, for completeness, the regional temperature-based indices from Lindegren and Checkley (2013). These indices were computed from seawater temperature averaged from 5 to 15 m depth during the spring CalCOFI surveys (SST<sub>spring</sub>) and during the four (winter, spring, summer, and fall) CalCOFI surveys (SST<sub>annual</sub>).

### Modelling approach

We first explored the correlation between the logarithmic recruitment success [ $\log(R/S)$ ] and the selected environmental variables using the Pearson linear correlation analysis. This exploratory analysis quantifies the covariability between the multiple variables and thereby guides subsequent model fitting.

We fit a variant of the linearized Ricker  $R$ - $S$  relationship (Quinn and Deriso, 1999), as implemented by Hill *et al.* (2011), but with the addition of environmental variables potentially related to recruitment, as in Jacobson and MacCall (1995). The data were fit to the following generalized linear model:

$$\log(\bar{R}) = \text{offset}(\log(S)) + \beta_0 + \beta_1 S + \sum_{j=1}^J \beta_{j+1} I_j, \quad (1)$$

where  $\bar{R}$  is the expected value of recruitment in million of fish,  $\text{offset}(\log(S))$  the logarithm of the age-1 + biomass with a fixed coefficient of 1 (McCullagh and Nelder, 1989),  $\beta_0$  the intercept,  $\beta_1$  the slope parameter for the  $S$ ; and the  $j$  environmental indices  $I_j$  have respective coefficients  $\beta_{j+1}$ . In Equation (1), error is evaluated only in the recruitment, allowing the use of many error structures for positive data, including the frequently used lognormal distribution (McCullagh and Nelder, 1989). The model was fit via a stepwise forward and backward selection procedure beginning with the  $S$  term, followed by the environmental variables with highest correlation with  $\log(R/S)$ . The model fit was evaluated with plots of the residuals to check for the homogeneity of the variance and independence of the residuals (McCullagh and Nelder, 1989). Contingent on the fit of the model, forward inclusion of the

variables was tested via the Akaike Information Criterion (AIC), which is an index that summarizes the quality of the fit and the parsimony of the model (Hobbs and Hilborn, 2006). To obtain a measure of global goodness of fit, we computed the square of the correlation coefficient between the logarithms of the fitted values and the logarithms of the observations. In a linear or additive model with a lognormal response, this quantity, named here as the “ $R^2$  equivalent,” corresponds to the unadjusted  $R^2$  statistic and to the percentage of deviance explained by the model. The models were fit using the library mgcv for R (Wood, 2006).

The predictive performance and the stability of the fitted models were assessed by cross-validation. For each of 1000 repetitions, three-quarters of the data were randomly selected (the training set) and used to fit the recruitment model; the model was used to predict the recruitment for the remaining quarter of the data (testing set). The  $R^2$  equivalent of the training and testing sets were recorded, as well as the AIC of the training set. Model overfitting is suspected if the  $R^2$  equivalent of the testing set is much less than that for the training set.

Because  $k$ , which is a proxy for total fecundity, depends significantly on whether the stock migrates north during summer to feed, the environmental Ricker model [Equation (1)] was fit with  $k$  only for the period when the stock is known to have undergone feeding migrations, i.e. for the period from 1999 to 2008. Including  $k$  in the best environmental Ricker model requires the model to be fitted with two extra parameters: one is a binary variable indicating whether  $k$  exists (i.e. pre- or post-1999), and the second is the slope relative to  $k$ , conditioned on  $k$  being available.

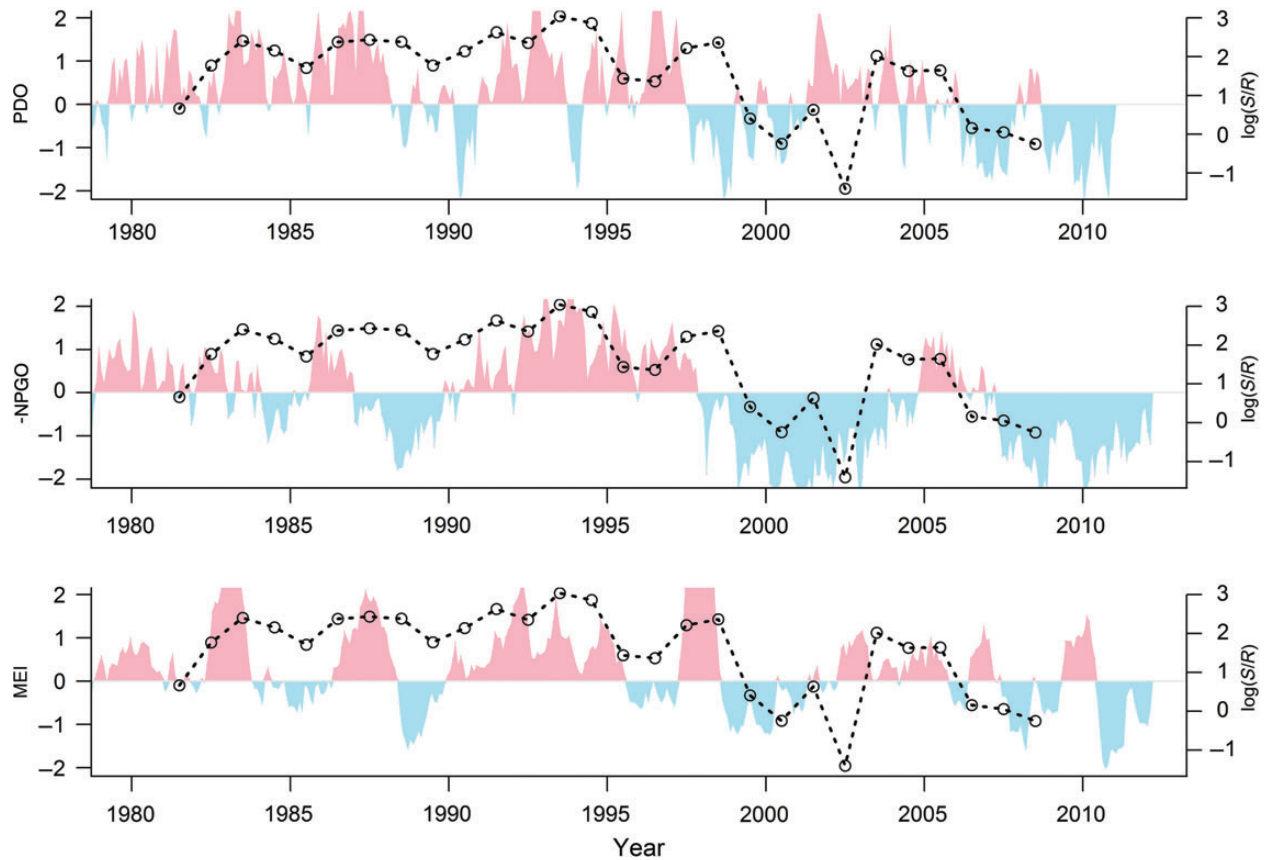
## Results

### Environmental indices and sardine reproductive success

Statistically significant correlations were found between  $\log(R/S)$  and each of the large-scale environmental indices, averaged during summer before the spawning season and during spring of the spawning and recruitment year (Figure 1, Table 1). The strongest correlation with a large-scale seasonal index was between the PDO during summer before the spawning season (PDO<sub>summer</sub>), followed by the PDO during the subsequent spring (PDO<sub>spring</sub>). The correlation was highest for the summed PDO<sub>summer</sub> and PDO<sub>spring</sub> indices (PDO<sub>combined</sub>). The temperature indices for the southern California region were also significantly correlated with  $\log(R/S)$ , but less than with PDO<sub>summer</sub> and PDO<sub>combined</sub> (Table 1). The various environmental variables are also significantly cross-correlated (Figure 1, Table 1), which reaffirms the known connections between them (Wells *et al.*, 2006).

### Regression analysis

Without environmental indices, Equation (1) is a biomass-only model. In this case,  $\beta_1$  is highly significant and has a negative slope, indicating a strong compensation of parental biomass on recruitment (Table 2, Figure 2). Based on its high linear correlation coefficient, PDO<sub>combined</sub> was the first environmental variable to be included in the model. It significantly reduced the unexplained variance of the biomass-only model and the residuals were homogeneously distributed with no signs of autocorrelation. Recruitment compensation was also reduced considerably (Table 2, Figure 2), but remained significant. Additional large- and regional-scale variables did not improve the model fit sufficiently to warrant their inclusion in the model. This is likely because the indices contain redundant information, as indicated by their high cross-correlations (Table 1). However, when tested in isolation, all the large-scale environmental indices proved to significantly reduce the proportion of unexplained



**Figure 1.** Logarithmic reproductive success (dashed line) from the 2010 assessment (Hill et al., 2010), overlaid on the monthly values of large-scale oceanographic monthly PDO index; North Pacific Gyre Oscillation index (NPGO); and Multivariate ENSO Index (MEI).

**Table 1.** Correlation matrix (*r*- and *p*-values) between the environmental indices, biomass of sardine age-1 and older (*S*), and logarithmic recruitment success [ $\log(R/S)$ ].

<i>p</i> -value	<i>r</i>	<i>S</i>	$\log(R/S)$	PDO <sub>spring</sub>	PDO <sub>summer</sub>	MEI <sub>spring</sub>	MEI <sub>summer</sub>	NPGO <sub>spring</sub>	NPGO <sub>summer</sub>	SST <sub>annual</sub>	SST <sub>spring</sub>	PDO <sub>combined</sub>
		****	-0.663	-0.395	-0.512	-0.316	-0.22	0.467	0.394	-0.364	-0.571	-0.538
		<0.001	****	0.537	0.673	0.53	0.43	-0.503	-0.49	0.62	0.531	0.718
		0.038	0.003	****	0.424	0.618	0.496	-0.576	-0.61	0.691	0.592	0.841
		0.005	<0.001	0.025	****	0.271	0.613	-0.309	-0.542	0.437	0.407	0.847
		0.102	0.004	<0.001	0.163	****	0.582	-0.499	-0.505	0.671	0.619	0.525
		0.26	0.022	0.007	0.001	0.001	****	-0.214	-0.512	0.531	0.368	0.658
		0.012	0.006	0.001	0.109	0.007	0.275	****	0.742	-0.338	-0.566	-0.523
		0.038	0.008	0.001	0.003	0.006	0.005	<0.001	****	-0.508	-0.485	-0.682
		0.057	<0.001	<0.001	0.02	<0.001	0.004	0.079	0.006	****	0.615	0.667
		0.001	0.004	0.001	0.032	<0.001	0.054	0.002	0.009	<0.001	****	0.591
		0.003	<0.001	<0.001	<0.001	0.004	<0.001	0.004	<0.001	<0.001	0.001	****

Spring indices are monthly averages from March through July of the recruitment year. Summer indices are monthly averages from July through October of the year before recruitment. Note the strong correlation between all environmental variables for each season, and the relative independence between the PDO<sub>summer</sub> and the NPGO<sub>spring</sub> and MEI<sub>spring</sub>. See Wells et al. (2006) for related analysis and discussion.

variance in recruitment in relation to the model using only the biomass as the predictor (Table 2). The models fit with the regional SST indices also explained large proportions of the recruitment variability (Table 2). However, they were more prone to overfitting than those using PDO<sub>summer</sub> or PDO<sub>combined</sub> (Table 3).

The model using the PDO<sub>combined</sub>:

$$\bar{R} = \exp(-4.194) \times S \times \exp(-8.511 \times 10^{-7} S + 0.267 \text{PDO}_{\text{combined}}) \tag{2}$$

had the highest proportion of the variance explained (for both the training and testing sets; Table 3), low AIC (Tables 2, 3), and independently distributed residuals. The global fit is very satisfactory and the *R*<sup>2</sup> equivalent is 0.85.

The three highest recruitments occurred during 1997, 1998, and 2003 when the sardine biomass was in the mid-range, i.e. ca. 750 000 tonnes (Figure 2). Below this optimal biomass value sardine production decreased quasi-linearly with biomass. Above this value, the parental biomass compensation effect forced recruitment into a plateau or decline (Figure 2). The shape of the curve does not

**Table 2.** Summary statistics for a subset of the evaluated environmental Ricker models [Equation (1)].

Explanatory variables	Linear coefficients	AIC	R <sup>2</sup> equivalent
S	-1.135e <sup>-06</sup>	501.8	77.1
S + MEI <sub>summer</sub>	-1.056e <sup>-06</sup> , 3.367e <sup>-01</sup>	498.3	80.7
S + MEI <sub>spring</sub>	-9.616e <sup>-07</sup> , 4.743e <sup>-01</sup>	494.9	81.8
S + NPGO <sub>summer</sub>	-9.098e <sup>-07</sup> , -2.595e <sup>-01</sup>	500.3	79.1
S + NPGO <sub>spring</sub>	-9.277e <sup>-07</sup> , -2.145e <sup>-01</sup>	501.1	78.6
S + PDO <sub>spring</sub>	-1.033e <sup>-06</sup> , 3.098e <sup>-01</sup>	499.3	81.6
S + PDO <sub>summer</sub>	-8.285e <sup>-07</sup> , 4.346e <sup>-01</sup>	495.9	83.3
S + SST <sub>spring</sub>	-9.384e <sup>-07</sup> , 3.261e <sup>-01</sup>	499.6	79.1
S + SST <sub>annual</sub>	-9.119e <sup>-07</sup> , 6.984e <sup>-01</sup>	491.9	84.2
S + PDO <sub>combined</sub>	-8.511e <sup>-07</sup> , 2.665e <sup>-01</sup>	492.1	85.1
PDO <sub>combined</sub>	3.469e <sup>-01</sup>	500.7	79.7

S is the parental biomass. The models were fitted using a logarithmic link function with a negative binomial distribution, with theta estimated during the fitting procedure. The linear coefficients represent the fitted parameters for the predictor variables. AIC is the Akaike Information Criterion. R<sup>2</sup> equivalent is the square of the coefficient of correlation between the logarithm of the observed recruitment and the logarithm of the fitted ones. None of the model residuals were autocorrelated. All model parameters were significant for  $\alpha = 0.1$  or lower. The number of observations is 28.

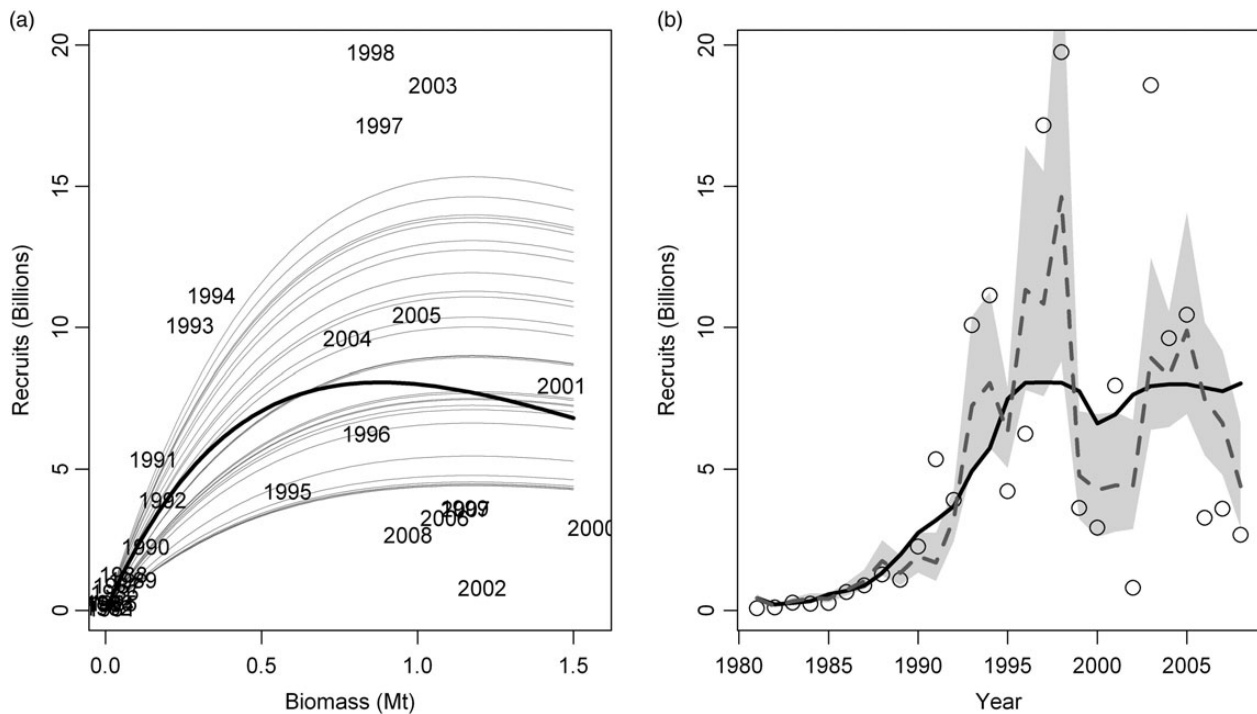
change significantly vs. the environmental index, but its scaling is extremely variable. For example, 1998 and 2002 had similar biomasses but the observed recruitments differed by 25-fold and the corresponding environmentally induced variations in the fitted model were 3.5 times higher than that of the lowest estimate (Figure 2).

Because *k*, a proxy for total fecundity, depends significantly on whether the stock migrates north during summer to feed, the environmental Ricker model was fit without *k* for the period from 1981 through 1998 [Equation (3a)] and with *k* for the period from 1999 to 2011 [Equation (3b)]:

**Table 3.** Cross-validation results for a subset of the models tested.

Explanatory variables	Training median AIC	Training median R <sup>2</sup> equivalent	Testing median R <sup>2</sup> equivalent
S	375.1	76.7	82.1
S + MEI <sub>summer</sub>	372.9	80.4	84.0
S + MEI <sub>spring</sub>	370.2	80.9	86.8
S + NPGO <sub>summer</sub>	374.2	79.5	79.4
S + NPGO <sub>spring</sub>	374.9	78.6	78.5
S + PDO <sub>spring</sub>	373.3	82.5	81.6
S + PDO <sub>summer</sub>	371.8	83.6	84.3
S + SST <sub>spring</sub>	375.4	79.0	81.6
S + SST <sub>annual</sub>	369.3	84.9	81.6
S + PDO <sub>combined</sub>	368.8	85.6	84.6
PDO <sub>combined</sub>	375.0	78.9	79.1

The 2003 and 1998 recruitments, which produced large residuals in the fitted models, were more often selected to the training vs. testing set and caused the median R<sup>2</sup> equivalent of the testing sets to be higher than that of the training sets in some of the fitted models.



**Figure 2.** (a) Environmental Ricker model (grey, corresponding to 1 line per year) vs. the static Ricker model (black), and (b) reconstruction of the recruitment time-series for the sardine stock from 1981 to 2008 (circles) using the static model (black) and environmental Ricker model (dashed grey) corresponding to the best model [Equation (2); Table 2], with 95% confidence intervals for predicted recruitment (grey area).

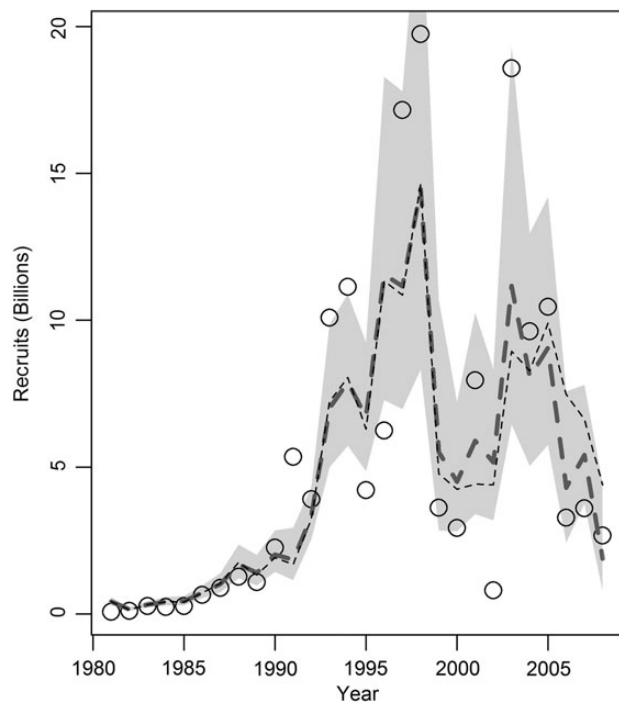
$$\bar{R} = \exp(-4.137) \times S \times \exp(-8.079 \times 10^{-7} S + 0.234 \text{PDO}_{\text{combined}}), \quad (3a)$$

$$\bar{R} = \exp(-11.826) \times S \times \exp(-8.079 \times 10^{-7} S + 0.234 \text{PDO}_{\text{combined}} + 4.71k). \quad (3b)$$

The coefficient for  $k$  is positive and statistically significant ( $p < 0.1$ ). The model including  $k$  [Equations (3a) and (3b)] has a higher  $R^2$  equivalent (86.2) and lower AIC (492.0) relative to the best model in Table 2, and the residuals for the 1999–2011 period are smaller (Figure 3).

## Discussion

All the models tested showed that environmental dynamics in the northeastern Pacific, particularly well captured by the PDO, significantly influenced sardine recruitment. Although sardine recruitment is strongly linked to the dynamics of their environment (e.g. Barnes *et al.*, 1992; Jacobson and MacCall, 1995; Jacobson *et al.*, 2001; MacCall, 2009; Zwolinski and Demer, 2012; this work), most studies assumed that sardine recruitment is predicated on the environment relevant to early (eggs and larvae) and juvenile life stages (Hjort, 1914; Lasker, 1981; MacCall, 2009; pers. comm. Rykaczewski and Checkley, 2008; McClatchie *et al.*, 2010; Lindegren and Checkley, 2013). For example, Lasker (1981) hypothesized that larval survival depends on the stability of the environment and the quality (species composition and size) and density of their food. MacCall (2004) associated large sardine recruitments to the retention of larvae in the nursery grounds,



**Figure 3.** Reconstruction of the recruitment time-series for the sardine stock from 1981 to 2008 (circles) using the best environmental Ricker model [Equation (2); Table 2; black dashed line]; and the best environmental Ricker model with  $k$  [Equation (3); grey dashed line] with 95% confidence intervals (grey area). The inclusion of  $k$  provides a better fit to the data after 2000.

which is maximized during low flows of the California Current. Also, Rykaczewski and Checkley (2008) observed that zooplankton size was related to the intensity of curl-driven upwelling offshore of southern California, which was correlated with surplus sardine production. Considered together, these findings relate strong sardine reproductive success (large recruitment) via larval survival to SSTs (Galindo-Cortes *et al.*, 2010; Lindegren and Checkley, 2013), the strength of the California Current (MacCall, 2009), and upwelling patterns (Rykaczewski and Checkley, 2008). To our minds, these characteristics recount complementary manifestations of the same basin-scale oceanographic phenomena that affect the dynamics of the biotic and abiotic environment in the California Current (Mantua *et al.*, 1997; Peterson and Schwing, 2003; Wells *et al.*, 2006; Keister *et al.*, 2011; Macias *et al.*, 2011) and that are indicated by positive PDO and *El Niño* indices (Macias *et al.*, 2011, 2012).

Although the survival of sardine larvae and juveniles is controlled by the physical environment (Cury *et al.*, 2000; Bakun, 2010), the availability of quality prey (Hjort, 1914), and predation and cannibalism for eggs and larvae (Ricker, 1954; Pitcher and Hart, 1982), we found that the highest correlations between sardine recruitment and the PDO-based index occur before the spawning season. Therefore, sardine recruitment appears to be not only related to the environment of the early life stages, but also to the cumulative effect of the environment on the adult sardine before spawning.

Sardine, perhaps more so than anchovy and other CPS, are “capital breeders”, i.e. their reproduction depends mainly on stored reserves, so parental condition may be vital for sustained reproductive effort (Kawasaki and Omori, 1995). Sardine spawning generally occurs after the period of highest fat accumulation (Zwolinski *et al.*, 2001; Garrido *et al.*, 2007). To spawn throughout a protracted season, with limited food ingestion, sardine depend greatly on the storage of high-energy lipids (Zwolinski *et al.*, 2001; Garrido *et al.*, 2007). The relationships between body fat quality and quantity and recruitment success are not well characterized nor perhaps broadly appreciated for sardine, but a significant positive correlation between the condition factor (i.e. body mass per cubic unit length) or lipid content and recruitment success were found for Pacific sardine in the California Current (Zwolinski and Demer, 2012) and Japan (Kawasaki and Omori, 1995), and European sardine (*Sardine pilchardus*; Rosa *et al.*, 2010). Zwolinski and Demer (2012) showed that  $k$  is positively correlated with recruitment, irrespective of the conditions necessary for larval and juvenile survival. Here, we showed that the  $k$  for migrating fish has a significant role on the prediction of sardine recruitment, supporting the expectation that the migration provides metabolic advantages. As previously shown for gadoids (Marshall *et al.*, 1999) and suggested for sardine (Kawasaki and Omori, 1995), the storage of fats in advance of the spawning season translates into increased fecundity, more resilient offspring, and potentially increased recruitment.

The statistically significant covariation between recruitment and the PDO during summer preceding the spring spawning is somewhat independent of the sardine biomass and condition factor. A potential explanation for why the environment before spawning might affect recruitment, irrespective of the condition factor (driven exclusively by weight changes), may be related to quality vs. quantity of their food. Oocyte formation requires not only fat but also proteins for structural components. These are known to depend on body tissue composition, which in turn depends on the biochemical contents of the prey (Riveiro *et al.*, 2004; Bode *et al.*, 2007; Garrido *et al.*, 2008). In the California Current,

perhaps the prey cascade resulting from a changing environment (Peterson and Schwing, 2003; Keister *et al.*, 2011) could vary the biochemical composition of oocytes and affect their survival. Alternatively, “preconditioning”, described by Schroeder *et al.* (2013), may explain how basin-scale oceanographic indices (e.g. PDO<sub>summer</sub>) predict regional near-term phenomena (e.g. spring-spawning success). These two hypotheses may be complementary and should be tested for sardine in the California Current.

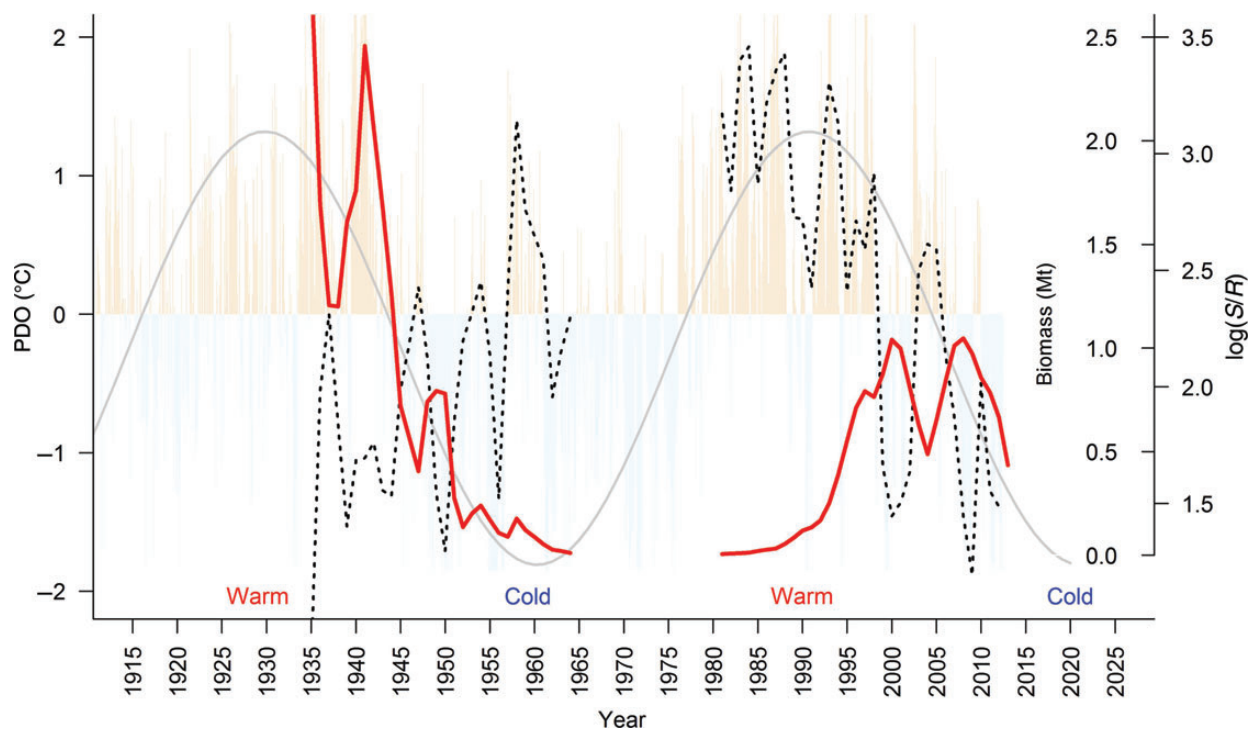
Despite the strong relationship we found between the PDO-based index and assessment-based estimates of sardine-stock recruitment, the latter may be compromised by an incomplete separation of the northern and southern stocks in the landings data (Jacobson and MacCall, 1995; Félix-Uraga *et al.*, 2005; Demer and Zwolinski, 2013). In particular, because the fisheries off Ensenada, Mexico, and San Pedro, CA, likely exploit two stocks (Félix-Uraga *et al.*, 2004, 2005; Demer and Zwolinski, 2013), the use of combined northern and southern stock landings in the assessment may have caused anomalously strong (e.g. 2003) or weak (e.g. 2002) estimates of recruitment that were not as evident in the survey time-series (Zwolinski *et al.*, 2012; Demer *et al.*, 2013; Zwolinski and Demer, 2013). Therefore, the recruitment time-series should be re-estimated with environmentally dependent stock partitioning (Demer and Zwolinski, 2013), and then this analysis should be revised. Improved accuracy in the estimated recruitment time-series could strengthen the performances of our models.

Notwithstanding the need to better differentiate the sardine stocks before an accurate evaluation of sardine recruitment (Félix-Uraga *et al.*, 2005; Hill *et al.*, 2006; Demer *et al.*, 2013; Demer and Zwolinski, 2013), periods of stock expansion and contraction in the 20th and 21st centuries are well explained by the environmental conditions indicated by the PDO (Chavez *et al.*, 2003; Zwolinski and

Demer, 2012; Deyle *et al.*, 2013). Although McClatchie (2012) did not find significant relationships between the PDO and sardine abundance on a longer time-scale, this may be due to uncertainty and noise in the data used to approximate the PDO (tree rings) and sardine abundance (fish-scale deposition), excessive smoothing of the data, or both.

The principal merits of using the PDO, vs. a small-scale index or survey-based measurements (e.g. the CalCOFI temperature index), is that it conveys sufficient information pertaining to the processes that were identified to directly affect recruitment (Lasker, 1981; Rykaczewski and Checkley, 2008; Chavez *et al.*, 2003) and it is readily and continuously available. Furthermore, from an operational standpoint, annually integrated survey-based metrics of the regional environment may require resources that could be directed to the sampling of the entire adult population. Finally, seasonal indices, as opposed to multiyear average indices, are better predictors of recruitment, because recruitment expectations are independent from the past year’s environment or average condition factor.

If the best stock recruitment model [Equation (2); Table 1] approximates reality, then the sardine abundance over the last century is governed by the cumulative effect of the annual recruitment success permitted by environmental conditions indicated by the PDO (Figure 4). Positive PDOs were correlated with large sardine recruitment, and consequentially biomass surpluses. Therefore, predominantly positive PDO periods (1920–1930s and 1980–1990s) were related to cumulatively larger sardine biomasses. Conversely, during prolonged periods with negative PDO values (1950–1970s and 2006 to the present), the reproductive success was low, and with total mortality exceeding recruitment, the population declined (Parrish, 2000; Zwolinski and Demer, 2012). More



**Figure 4.** The PDO index indicating positive (pink) and negative (light blue) monthly values; the 60-year periodic component of the PDO projected to 2020 (grey line; Zwolinski and Demer, 2012); the assessment estimated sardine biomass (red); and the predicted logarithmic stock – recruitment ratio (dashed line).

specifically, the decline in the sardine stock around 1935 resulted from low recruitment success due to high biomasses, in conjunction with high exploitation (Radovich, 1982; Parrish, 2000; Zwolinski and Demer, 2012). During the mid-1940s, the PDO locked into a negative phase, high exploitation continued, and the stock plummeted. During the next three decades, the PDO was largely negative, the reproductive success of sardine was low and sardine continued to decline until they were virtually absent from all of their historical fishing grounds and their biomass was untraceable (Parrish, 2000).

Only in the 1980s, when the PDO became mainly positive again and fishing mortalities were low (Hill *et al.*, 2010), the population recovered at a rate of as much as 30% per year (Figure 4). The direct effect of the environment on the dynamics of the stock can be seen in the rapid decline in the biomass from 1999 through 2003, in agreement with 4 years of negative PDO values. The rate of decrease, 16% per year, is higher than the exploitation rate (~11% per year; Hill *et al.*, 2010), so recruitments were less than total mortality, even in the absence of fishing. Three strong year classes (2003–2005) contributed to a temporary resurgence of the stock through 2007 and dominated the stock through 2011 when a smaller 2009/2010 cohort appeared (Demer and Zwolinski, 2012; Zwolinski and Demer, 2012).

After 1998, the PDO was increasingly negative. In particular, between 1999 and December 2012, 61% of the monthly PDO values were negative; and between January 2008 and December 2012, 85% were negative (in contrast, between 1981 and 1998, only 22% of the monthly PDO values were negative). Between 1999 and 2011, in concert with this relatively cold period, the assessment-derived reproductive success has been, on average, 30% of that observed in the previous 20 years. If we exclude from this analysis the three good recruitments between 2003 and 2005, observed during a short period with a positive PDO, the recruitment success was, on average, 14% of that observed during the sardine population expansion in the 1980s and the 1990s.

Although the behaviour of the PDO and that of multiple fish populations are often complicated by high frequency and unpredictable variability (Peterson and Schwing, 2003; Overland *et al.*, 2008; Black *et al.*, 2011), the recent cold period in the northeast Pacific appears to be in agreement with the dominant ~60-year component of the PDO, which is trending negative and its minimum is expected to occur between 2020 and 2025 (Figure 4; Zwolinski and Demer, 2012). If this signal continues to dominate in the future, and the environmental conditions that the PDO represents continue to predict sardine recruitment, the productivity of the stock will be low and yields will be reduced over the next decade. During extended periods of low recruitment, exploitation could exacerbate a decline in the stock (Jacobson and MacCall, 1995; PFMC, 1998) and both delay and stunt its recovery during the next period with favourable environmental conditions (Zwolinski and Demer, 2012). However, if an adequate seed biomass is maintained during the periods of average low productivity, unpredictable, short-term positive PDO episodes could intermittently yield surplus biomass.

## Conclusion

We showed that the dynamics in oceanographic conditions described by fluctuations of the PDO explain the succession of sardine recruitment in the California Current during the last three decades. We showed that PDO-based indices for both the summer feeding season ( $PDO_{\text{summer}}$ ) and the following spring-spawning season ( $PDO_{\text{spring}}$ ) covary with sardine recruitment; and we provided an environmental Ricker model, parameterized with a “dual-phase” summer and spring PDO index ( $PDO_{\text{combined}}$ ) and a condition

factor to predict sardine recruitment. This implies that prespawning density-dependent energy storage is an additional mechanism for the compensatory effect implicit in the Ricker model fitted to sardine recruitment. All of these findings support our hypothesis that high recruitment occurs when oceanographic conditions are favourable for the parents during their summer feeding season, their condition factor is high, and the oceanographic conditions during the following spring-spawning season maximize early life stage survival. This data-supported hypothesis significantly augments the century-old theory that the reproductive success of coastal pelagic fish is governed by early life stage survival (Hjort, 1914; Lasker, 1978). Parental condition matters, too.

## Acknowledgements

We thank Sean Hayes, Brian Wells, Nate Mantua, Bill Perrin, and Russ Vetter from SWFSC, and three anonymous reviewers and Jose Hidalgo for their constructive critiques and suggestions. We thank Kevin Hill and everyone involved in the assessment of the Pacific sardine. We also thank the persons responsible for producing and maintaining the environmental data time-series.

## References

- Alheit, J., and Bakun, A. 2010. Population synchronies within and between ocean basins: apparent teleconnections and implications as to physical-biological linkage mechanisms. *Journal of Marine Systems*, 79: 267–285.
- Bakun, A. 2010. Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: conceptual templates and schematic constructs. *Journal of Marine Systems*, 79: 361–373.
- Barnes, J. T., MacCall, A. D., Jacobson, L. D., and Wolf, P. 1992. Recent population trends and abundance estimates for the Pacific sardine (*Sardinops sagax*). CALCOFI Reports, 33: 60–75.
- Baumgartner, T., Soutar, A., and Ferreira-Bartrina, V. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. CALCOFI Reports, 33: 24–40.
- Black, B. A., Schroeder, I. D., Sydeman, W. J., Bograd, S. J., Wells, B. K., and Schwing, F. B. 2011. Winter and summer upwelling modes and their biological importance in the California Current Ecosystem. *Global Change Biology*, 17: 2536–2545.
- Bode, A., Alvarez-Ossorio, M. T., Cunha, M. E., Garrido, S., Peleteiro, J. B., Porteiro, C., Valdes, L., *et al.* 2007. Stable nitrogen isotope studies of the pelagic food web on the Atlantic shelf of the Iberian Peninsula. *Progress in Oceanography*, 74: 115–131.
- Chavez, F. P., Ryan, J., Lluch-Cota, S. E., and Niquen, C. M. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science*, 299: 217–221.
- Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quinones, R. A., Shannon, L. J., and Verheye, H. M. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, 57: 603–618.
- Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 670–680.
- Demer, D. A., Zwolinski, J. P., Byers, K., Cutter, G. R., Jr, Renfree, J. S., Sessions, S. T., and Macewicz, B. J. 2012. Seasonal migration of Pacific sardine (*Sardinops sagax*) in the California Current ecosystem: prediction and empirical confirmation. *Fishery Bulletin*, 110: 52–70.
- Demer, D. A., and Zwolinski, J. P. 2013. Corroboration and refinement of a method for differentiating landings from two stocks of Pacific sardine (*Sardinops sagax*) in the California Current. *ICES Journal of Marine Science*.
- Demer, D. A., and Zwolinski, J. P. 2012. Reply to MacCall *et al.*: Acoustic-trawl survey results provide unique insight to sardine



- stock decline. Proceedings of the National Academy of Sciences of the USA, 109: E1132–E1133.
- Demer, D. A., Zwolinski, J. P., Cutter, G. R., Jr, Byers, K., Macewicz, B. J., and Hill, K. T. 2013. Sampling selectivity in acoustic-trawl surveys of Pacific sardine (*Sardinops sagax*) biomass and length distribution. ICES Journal of Marine Science.
- Deyle, E. R., Fogarty, M., Hsieh, C. H., Kaufman, L., MacCall, A. D., Munch, S. B., Perretti, C. T., *et al.* 2013. Predicting climate effects on Pacific sardine. Proceedings of the National Academy of Sciences of the USA, 110: 6430–6435.
- DeYoung, B., Barange, M., Beaugrand, G., Harris, R., Perry, R. I., Scheffer, M., and Werner, F. 2008. Regime shifts in marine ecosystems: detection, prediction and management. Trends in Ecology and Evolution, 23: 402–409.
- Di Lorenzo, E., Schneider, N., Cobb, K. M., Franks, P. J. S., Chhak, K., Miller, A. J., McWilliams, J. C., *et al.* 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters, 35: L08607.
- Félix-Uraga, R., Gómez-Muñoz, V. M., Quiñónez-Velázquez, C., and García-Franco, W. 2004. On the existence of Pacific sardine groups off the west coast of Baja California and Southern California. CALCOFI Reports, 45: 146–151.
- Félix-Uraga, R., Gómez-Muñoz, V. M., Quiñónez-Velázquez, C., Melo-Barrera, F. N., Hill, K. T., and García-Franco, W. 2005. Pacific sardine (*Sardinops sagax*) stock discrimination off the west coast of Baja California and southern California using otolith morphometry. CALCOFI Reports, 46: 113–121.
- Fréon, P., Cury, P., Shannon, L., and Roy, C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bulletin of Marine Science, 76: 385–462.
- Galindo-Cortes, G., De Anda-Montanez, J. A., Arreguin-Sanchez, F., Salas, S., and Balart, E. F. 2010. How do environmental factors affect the stock-recruitment relationship? The case of the Pacific sardine (*Sardinops sagax*) of the northeastern Pacific Ocean. Fisheries Research, 102: 173–183.
- Ganias, K., Somarakis, S., Koutsikopoulos, C., and Machias, A. 2007. Factors affecting the spawning period of sardine in two highly oligotrophic seas. Marine Biology, 151: 1559–1569.
- Garrido, S., Rosa, R., Ben-Hamadou, R., Cunha, M. E., Chicharo, M. A., and van der Lingen, C. D. 2007. Effect of maternal fat reserves on the fatty acid composition of sardine (*Sardina pilchardus*) oocytes. Comparative Biochemistry and Physiology B: Biochemistry and Molecular Biology, 148: 398–409.
- Garrido, S., Rosa, R., Ben-Hamadou, R., Cunha, M. E., Chicharo, M. A., and van der Lingen, C. D. 2008. Spatio-temporal variability in fatty acid trophic biomarkers in stomach contents and muscle of Iberian sardine (*Sardina pilchardus*) and its relationship with spawning. Marine Biology, 154: 1053–1065.
- Hill, K., Crone, P. R., Lo, N. C. H., Macewicz, B. J., Dorval, E., McDaniel, J. D., and Gu, Y. 2011. Assessment of the Pacific sardine resource in 2011 for US management in 2012. US Department of Commerce. NOAA Technical Memorandum, NMFS-SWFSC-487.
- Hill, K. T., Lo, N. C. H., Macewicz, B. J., Crone, P. R., and Félix-Uraga, R. 2010. Assessment of the Pacific sardine resource in 2010 for US management in 2011. US Department of Commerce. NOAA Technical Memorandum, NMFS-SWFSC-469. 137 pp.
- Hill, K. T., Lo, N. C. H., Macewicz, B. J., and Félix-Uraga, R. 2006. Assessment of the Pacific sardine (*Sardinops sagax caerulea*) population for US management in 2007. NOAA Technical Memorandum, NMFS-SWFSC-396. 79 pp.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions Conseil International pour l'Explorations de la Mer, 1: 5–38.
- Hobbs, N. T., and Hilborn, R. 2006. Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. Ecological Applications, 16: 5–19.
- Irvine, J. R., and Fukuwaka, M. A. 2011. Pacific salmon abundance trends and climate change. ICES Journal of Marine Science, 68: 1122–1130.
- Jacobson, L. D., De Oliveira, J. A. A., Barange, M., Cisneros-Mata, M. A., Felix-Uraga, R., Hunter, J. R., Kim, J. Y., *et al.* 2001. Surplus production, variability, and climate change in the great sardine and anchovy fisheries. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1891–1903.
- Jacobson, L. D., and MacCall, A. D. 1995. Stock recruitment models for Pacific sardine (*Sardinops sagax*). Canadian Journal of Fisheries and Aquatic Sciences, 52: 2062–2062.
- Kawasaki, T., and Omori, M. 1995. Possible mechanism underlying fluctuation in the Far Eastern sardine population inferred from time series of two biological traits. Fisheries Oceanography, 4: 238–242.
- Keister, J. E., Di Lorenzo, E., Morgan, C. A., Combes, V., and Peterson, W. T. 2011. Zooplankton species composition is linked to ocean transport in the Northern California Current. Global Change Biology, 17: 2498–2511.
- King, J. R. (Ed.) 2005. Report of the study group on fisheries and ecosystem responses to recent regime shifts. PICES Scientific Report, 28, 162 pp.
- King, J. R., Agostini, V. N., Harvey, C. J., McFarlane, G. A., Foreman, M. G. G., Overland, J. E., Di Lorenzo, E., *et al.* 2011. Climate forcing and the California Current ecosystem. ICES Journal of Marine Science, 68: 1199–1216.
- Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapports et Procès-Verbaux des Réunions Conseil International pour l'Explorations de la Mer, 173: 212–230.
- Lasker, R. 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. In Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries, pp. 80–88. Ed. by R. Lasker. Washington Sea Grant, Seattle.
- Lindegren, M., and Checkley, D. M., Jr. 2013. Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised. Canadian Journal of Fisheries and Aquatic Sciences, 70: 245–252.
- MacCall, A. D. 1979. Population estimates for the warming years of the Pacific sardine fishery. CALCOFI Reports, 20: 72–82.
- Maccall, A. D. 2009. Mechanisms of low-frequency fluctuations in sardine and anchovy populations. In Climate Change and Small Pelagic Fish, pp. 285–299. Ed. by D. M. Checkley, Jr, J. Alheit, Y. Oozeki, and C. Roy. Cambridge University Press, New York.
- MacCall, A. D., Batchelder, H., King, J. R., Mackas, D. L., Mantua, N., McFarlane, G. A., Perry, I., *et al.* 2005. Recent ecosystem changes in the California Current System. PICES Scientific Report, 28. 162 pp.
- Macias, D., Franks, P. J. S., Ohman, M. D., and Landry, M. R. 2012. Modeling the effects of coastal wind- and wind-stress curl-driven upwellings on plankton dynamics in the Southern California current system. Journal of Marine Systems, 94: 107–119.
- Macias, D., Landry, M. R., Gershunov, A., Miller, A. J., and Franks, P. J. S. 2011. Climatic control of upwelling variability along the western North-American Coast. PLoS One, 7: e30436.
- Mantua, N., Hare, S. R., Zhang, Y., Wallace, J. M., and Francis, R. C. 1997. A Pacific decadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society, 78: 1069–1079.
- Marshall, C. T., Yaragina, N. A., Lambert, Y., and Kjesbu, O. S. 1999. Total lipid energy as a proxy for total egg production by fish stocks. Nature, 402: 288–290.
- McClatchie, S. 2012. Sardine biomass is poorly correlated with the Pacific Decadal Oscillation off California. Geophysical Research Letters, 39: L13703.
- McClatchie, S., Goericke, R., Auad, G., and Hill, K. 2010. Re-assessment of the stock-recruit and temperature-recruit relationships for Pacific sardine (*Sardinops sagax*). Canadian Journal of Fisheries and Aquatic Sciences, 67: 1782–1790.

- McCullagh, P., and Nelder, J. A. 1989. Generalized Linear Models. Chapman and Hall, London.
- Norton, J. G., and Mason, J. E. 2005. Relationship of California sardine (*Sardinops sagax*) abundance to climate-scale ecological changes in the California Current System. CALCOFI Reports, 46: 83–92.
- Overland, J., Rodionov, S., Minobe, S., and Bond, N. 2008. North Pacific regime shifts: definitions, issues and recent transitions. Progress in Oceanography, 77: 92–102.
- Overland, J. E., Alheit, J., Bakun, A., Hurrell, J. W., Mackas, D. L., and Miller, A. J. 2010. Climate controls on marine ecosystems and fish populations. Journal of Marine Systems, 79: 305–315.
- Parrish, R. H. 2000. A Monterey sardine story. J. B. Phillips Historical Fisheries Report, 1: 2–4.
- Perry, R. I., Cury, P., Brander, K., Jennings, S., Mollmann, C., and Planque, B. 2010. Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. Journal of Marine Systems, 79: 427–435.
- Peterson, W. T., and Schwing, F. B. 2003. A new climate regime in north-east pacific ecosystems. Geophysical Research Letters, 30: 1896.
- PFMC. 1998. Amendment 8 (to the northern anchovy fishery management plan) incorporating a name change to: the coastal pelagic species fishery management plan. Management Council, Portland, OR.
- Pitcher, T. J., and Hart, P. B. 1982. Fisheries Ecology. AVI Publishing, Westport, CT.
- Quinn, T. J., and Deriso, R. B. 1999. Quantitative Fish Dynamics. Oxford University Press, New York.
- Radovich, J. 1982. The collapse of the California sardine fishery: what have we learned? CALCOFI Reports, 23: 56–78.
- Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada, 11: 559–623.
- Riveiro, I., Guisande, C., Maneiro, I., and Vergara, A. R. 2004. Parental effects in the European sardine *Sardina pilchardus*. Marine Ecology Progress Series, 274: 225–234.
- Rosa, R., Gonzalez, L., Broitman, B. R., Garrido, S., Santos, A. M. P., and Nunes, M. L. 2010. Bioenergetics of small pelagic fishes in upwelling systems: relationship between fish condition, coastal ecosystem dynamics and fisheries. Marine Ecology Progress Series, 410: 205–218.
- Rykaczewski, R. R., and Checkley, D. M., Jr. 2008. Influence of ocean winds on the pelagic ecosystem in, upwelling regions. Proceedings of the National Academy of Sciences of the USA, 105: 1965–1970.
- Schroeder, I. D., Black, B. A., Sydeman, W. J., Bograd, S. J., Hazen, E. L., Santora, J. A., and Wells, B. K. 2013. The North Pacific High and wintertime pre-conditioning of California current productivity. Geophysical Research Letters, 40: 541–546.
- Wells, B. K., Grimes, C. B., Field, J. C., and Reiss, C. S. 2006. Covariation between the average lengths of mature coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) and the ocean environment. Fisheries Oceanography, 15: 67–79.
- Wolter, K., and Timlin, M. S. 1998. Measuring the strength of ENSO events: how does 1997/98 rank? Weather, 53: 315–324.
- Wood, S. 2006. Generalized Additive Models: an Introduction with R. Texts in Statistical Sciences. Chapman and Hall/CRC, Boca Raton, FL. 391 pp.
- Zwolinski, J., Stratoudakis, Y., and Soares, E. 2001. Intra-annual variation in the batch fecundity of sardine off Portugal. Journal of Fish Biology, 58: 1633–1645.
- Zwolinski, J. P., and Demer, D. A. 2012. A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. Proceedings of the National Academy of Sciences of the USA, 109: 4175–4180.
- Zwolinski, J. P., and Demer, D. A. 2013. Measurements of natural mortality of Pacific sardine. ICES Journal of Marine Science.
- Zwolinski, J. P., Demer, D. A., Byers, K. A., Cutter, G. R., Renfree, J. S., Sessions, S. T., and Macewicz, B. J. 2012. Distributions and abundances of Pacific sardine (*Sardinops sagax*) and other pelagic fishes in the California Current ecosystem during spring 2006, 2008, and 2010, estimated from acoustic-trawl surveys. Fishery Bulletin US, 110: 110–122.
- Zwolinski, J. P., Emmett, R. L., and Demer, D. A. 2011. Predicting habitat to optimize sampling of Pacific sardine (*Sardinops sagax*). ICES Journal of Marine Science, 68: 867–879.

Handling editor: Manuel Hidalgo